SOME ASPECTS OF THE REPRODUCTIVE STRATEGY
OF *ILISHA AFRICANA* (BLOCH, 1795)
(TELEOSTEI, CLUPEIDAE)
IN QUA IBOE ESTUARY, NIGERIA

by

Richard P. KING (1)

ABSTRACT. - Some aspects of the reproductive strategy of *Ilisha africana* (Bloch, 1795) in Qua Iboe estuary, Nigeria, were studied between November, 1987 and October, 1988 inclusive. *I. africana* is a monomorphic species. Sex ratio was strongly female-biased with no marked seasonal switches but there were significant ontogenetic and monthly heterogeneities. Females attained sexual maturity at a median size of 15.4 cm TL (range 6.5-21.0 cm TL). Gonadosomatic index decreased with increasing fish size and fat index. Investment in egg weight increased with ovary weight and gonadosomatic index but decreased with increasing total/standard lengths and total/somatic weights. Breeding was year-round, with maximum and minimum intensities in December and March respectively. Mean fecundity was 6,716 eggs (range 2,142-12, 602 eggs); it increased with fish total/standard lengths and total/somatic weights but decreased with increasing egg weight, gonadosomatic and condition indices. These attributes depicted trade-offs between growth and reproductive investment and between the latter and lipid energy reserves. There were also trade-offs between fecundity and reproductive investment, egg quality and the relative well-being of the fish. The reproductive life history of *I. africana* which incorporates the r- and k-selection traits, is considered as a strategy adopted to equilibrate the optimization of reproductive success and enhanced potential of progeny survival.

RÉSUMÉ. - Quelques aspects de la stratégie de reproduction de *Ilisha africana* (Bloch, 1795) dans l'estuaire de la rivière Qua Iboe, Nigéria, ont été étudiés de novembre 1987 à octobre 1988 inclus. *I. africana* est une espèce monomorphe. Le sex-ratio est fortement en faveur des femelles et sans changement marqué entre les saisons, mais on observe des hétérogénéités ontogénétique et mensuelle significatives. Les femelles atteignent leur maturité sexuelle à une taille moyenne de 15,4 cm LT (de 6,5 à 21,0 cm LT). L'indice gonadosomatique diminue lorsque la taille du poisson et l'indice de matières grasses augmentent. Le poids des oeufs augmente en même temps que le poids des ovaires et que l'indice gonadosomatique, mais il diminue lorsque la taille (longueurs totale/standard) et le poids (total/somatique) augmentent. La reproduction se déroule toute l'année avec des intensités maximale en décembre et minimale en mars. La fécondité moyenne est de 6716 oeufs (de 2142 à 12602); elle augmente avec la taille (longueurs totale/standard) et le poids (total/somatique), mais diminue lorsque le poids des oeufs, l'indice gonadosomatique et l'indice de condition augmentent. Ces résultats révèlent l'existence d'échanges entre croissance et effort de reproduction et entre ce dernier et les réserves énergétiques en lipides. Il y a aussi des échanges entre fécondité et effort de reproduction, qualité des oeufs et bien-être relatif du poisson. Le déroulement de la reproduction de *I. africana*, qui incorpore les règles de sélection r- et k-, est considéré comme une stratégie adoptée pour équilibrer l'optimisation du succès reproductif et améliorer le potentiel de survie de la progéniture.

Key-words. - Clupeidae, *Ilisha africana*, Nigeria, Sex ratio, Reproductive effort, Breeding seasonality, Fecundity, Trade-off.

(1) Department of Zoology and Fisheries, University of Cross River State, PMB 1017, Uyo, NIGERIA.

The shoaling pelagic clupeid, *Ilisha africana* (Bloch, 1795), occurs in the Atlantic coastal waters of the Gulf of Guinea, from Senegal to Zaire. It is most abundant in the Nigerian inshore waters (Williams, 1968) at depths of 20-30 m although its bathymetric distribution is 10-50 m (Marcus and Kusemiju, 1984). *I. africana* forms an important proportion of the catches of artisanal fishermen throughout the Nigerian coastal waters and constitutes a major protein source for the riparian communities. In the Qua Iboe estuary, between the Niger delta and Cross river estuary in Nigeria, the artisanal fishery is specially for *Ilisha africana* (Marcus *et al.*, 1984; pers. obs.).

In spite of its wide geographic distribution and economic value, not much is known about the biology of *I. africana*. In Nigeria, available information is based on studies carried out on the populations in Lagos lagoon (Fagada and Olaniyan, 1973) and off the Lagos coast (Tobor, 1966; Marcus and Kusemiju, 1984; Marcus, 1986) in the West. There are few or no biological records on this species elsewhere along the coastal waters of Nigeria.

This paper is intended to examine aspects of the reproductive strategy of *Ilisha africana* in the Qua Iboe estuary, southeastern Nigeria. The reproductive strategy of a fish species embodies an aggregate of reproductive attributes which it manifests so as to maximize its reproductive success in the form of off-springs; such attributes include *inter alia*, age and size at first maturity, reproductive effort, egg size, fecundity and breeding seasonality (Roff, 1982; Mills and Eloranta, 1985b; Goldschmidt, 1989a, b; Goldschmidt and Witte, 1989). The present study addresses some of these traits and the results are discussed in light of the current concepts and theories of reproductive strategies. Background information on the reproductive strategy of *I. africana* is central to the planning and implementation of rational exploitation and conservation programs of its wild stocks, in view of its value as food throughout its geographic range.

Study area

Qua Iboe river (7°30′ - 8°20′ W; 4°30′ - 5°30′ N) (Fig. 1) is the dominant hydrographic feature in Akwa Ibom State, Nigeria. It drains a basin area of about 7,092 km^2 and the main river course covers a distance of 150 km from its source at Umudike (7°33′ W; 5°29′N; elevation 122 m above sea level (asl)) in Imo State, to where it empties into the southeastern part of the Bight of Bonny in the Gulf of Guinea at an elevation of less than 24 m asl.

The geomorphology of the southern-most part of the catchment area consists of fine sandy coastal beach ridges covering about 560 km^2. The estuary comprises tidal creeks, small mixohaline lagoons and fringing mangrove swamps. The depth of the main estuary is 0.5-9 m while the tidal amplitude is 1-3 m. The macrophytes of the coastal mangrove swamp are predominated by *Rhizophora harrizonii*, *Rhizophora mangle*, *Rhizophora racemosa*, *Avicennia africana* and *Laguncularia racemosa*. Few stands of *Acrostichum aureum*, *Nypa fruticans*, *Phoenix reclinate* and *Drepanocarpus lunatus* also occur in some places.

The climate of the estuarine zone is typical of the equatorial hot-humid regime with year-round precipitation. Two seasons (dry and wet) are however discerned in the area. The dry season extends from November to February, with peak in January. The wet season ranges between March and October, with peak in August. Further details on the study area are given in Tahal Consultants (1979), Enyenihi *et al.* (1988) and King *et al.* (in press).

MATERIALS AND METHODS

Between November, 1987 and October, 1988, monthly samples of *Ilisha africana* were obtained from artisanal fishermen who landed their catch at Ibeno
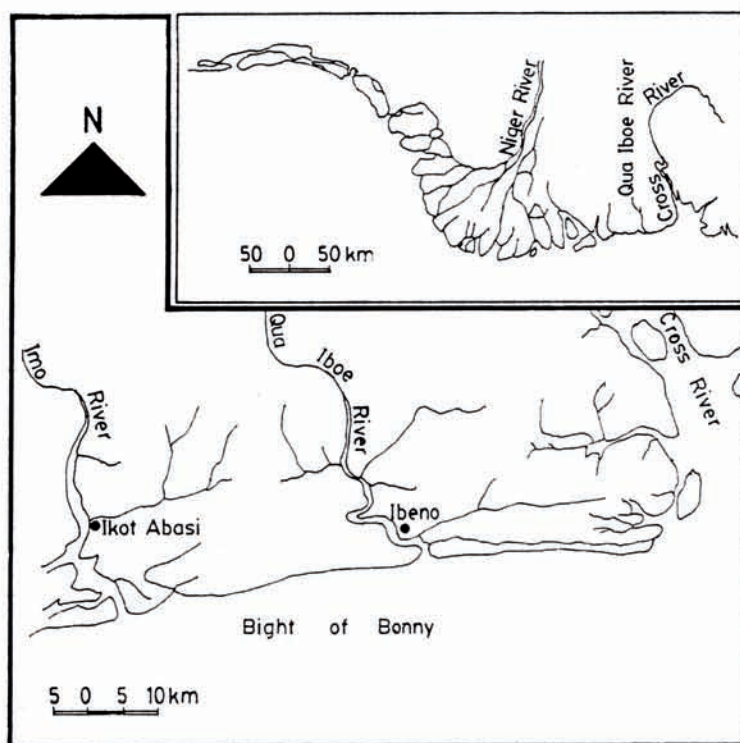
Fig. 1. - Map of southeastern coast of Nigeria showing the Qua Iboe estuary. Inset: map of the coast of Nigeria showing the location of Qua Iboe river.

fishing terminal (Fig. 1). Fishing was effected mainly by the use of encircling gill-nets (50-70 mm stretched mesh) operated from dug-out canoes (7-12 m overall length) some of which were powered by 15-40 HP outboard motor engines.

The specimens were transported to the laboratory where they were measured to the nearest 0.1 cm (total and standard lengths) and weighed to the nearest 0.1 g (total weight). They were dissected and sex was established on the basis of macroscopic examination of gonads. Ovaries from each specimen were weighed to the nearest 0.01 g and the stage of development recorded according to Lagler (1978). The somatic weight of each specimen was calculated as total body weight minus ovary weight and the gonadosomatic index, as weight of ovary relative to total body weight, expressed as a percentage. Fifty specimens of each sex were carefully examined for sex-based morphological differences.

To determine fecundity (total number of ripe eggs in the ovaries prior to spawning; absolute fecundity of Begenal and Braum, 1978), ripe ovaries from each of 31 females were individually preserved in labelled vials containing 4% formalin until the eggs hardened (over 2-4 weeks). The vials were periodically agitated to ensure the separation of the eggs from ovarian tissue. The eggs were later air-dried on absorbent paper for 24 h at 27-30°C ambient temperature. The fecundity was determined by weighing all the eggs from each pair of ovaries and then two random subsamples of 200 eggs each; the ratio of total weight of eggs to mean weight of subsamples was multiplied by 200 to give an estimate of the absolute fecundity of each fish (Wilkinson and Jones, 1977).

The relationship between fecundity (F) and each of the independent variable (x_i) (total length (TL), standard length (SL), total weight (W_t), somatic weight (W_s), ovary weight (W_o), individual egg weight (W_e), gonadosomatic index (GSI) and condition index $(K = W_t.100/(TL)^3)$) was represented by the expression:

$$F = a.X_i^b \tag{1}$$

where a = a constant and b = regression coefficient, both of which were determined by least square regression analysis using double-log-transformed data.

The presence and amount of visceral fat deposits were determined for females caught throughout the study period. The amount was estimated semi-quantitatively according to an arbitrary 0-20 points scheme (cf. Nikolsky, 1963); thus ratings of 0, 5, 10, 15 and 20 points were assigned to absence, scanty, light, moderate and heavy fat deposits respectively; intermediate points were also awarded in cases of intermediate amounts of fat. The fat index was then calculated as mean points per fish.

RESULTS

Sexual dimorphism

There was no obvious sexual dimorphism in the morphological features of *Ilisha africana*. Colour dimorphism was also not discerned. Sexually active females were, however, slightly heavier than similarly-sized males (paired t-test: t = 6.202, 12 df, P < 0.001: Table I), this weight difference being apparently due to the heavier female ovaries *vis-à-vis* the tests.

Total length	Total weight (g)	
(cm)	Males	Females
13.0	13.6	14.5
13.8	17.6	17.7
14.0	19.0	20.7
14.2	19.3	23.2
15.0	24.3	26.3
15.1	23.8	28.8
15.9	30.6	33.3
16.0	29.0	34.0
16.5	34.2	35.7
16.9	35.1	40.0
19.0	50.7	55.7
19.8	54.1	55.9
20.5	56.4	60.0

Table I. - Comparison of the weights of similarly-sized males and sexually active females of *I. africana*.
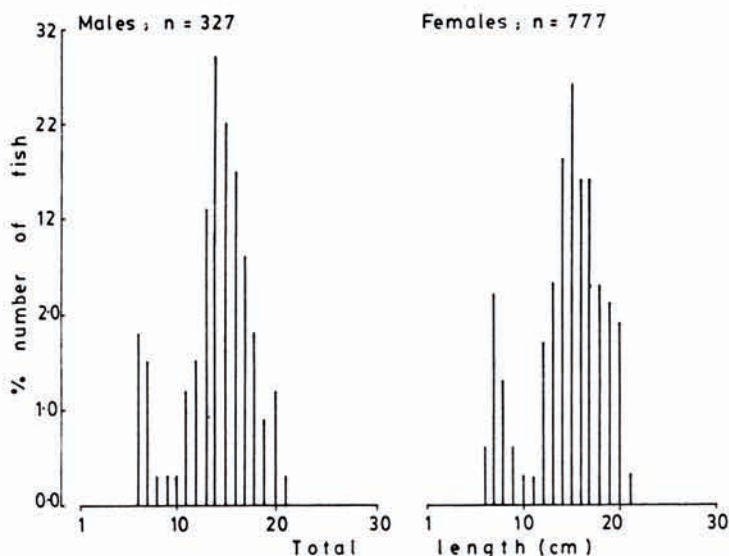
Fig. 2. - Size structure of male and female populations of *I. africana* in Qua Iboe estuary.

Population structure

Ilisha africana of < 6 cm TL could not be reliably sexed by inspecting the gonads and were thus considered as prereproductives or juveniles. The length-frequency distributions of adults (≥ 6 cm TL) per sex (Fig. 2) showed no marked size dimorphism between the males and females; both sexes occurred over the entire range of body size (6-21 cm TL) examined. Man-Whitney statistic revealed no significant sex-based differences in the length-frequency distribution (Man-Whitney $U = 116$, $n_1 = n_2 = 16$, $P > 0.05$). There were two size-classes in each sex; in the male population, modes were recorded at 6 and 14 cm TL while in that of the female, modes occurred at 7 and 15 cm TL. Average sizes of males and females were 14.4 cm TL and 14.8 cm TL respectively.

Sex ratio

Of the 1,104 adult specimens examined, 327 (29,6%) were males and 777 (70.4%) females, giving an overall male:female ratio of 1.0:2.4 which was significantly different from unity (Goodness-of-fit $X^2 = 183.424$, 1 df, $P < 0.001$) with a strong bias in favour of females.

Plasticity in the proportions of males and females relative to body size are illustrated in figure 3; Brandt and Snedecor's contingency X^2 test (Bailey, 1959) showed significantly heterogeneity ($X^2 = 57.973$, 15 df, $P < 0.001$) in the sex ratios of the various size-classes. Females dominated in all the size-classes except in the 6, 12 and 13 cm TL classes when males slightly outnumbered females. Peak female dominance occurred in the 7-10 cm TL and 14-21 cm TL size ranges.

Monthly variations in the proportions of male and female *Ilisha africana* are presented in figure 4; the male:female ratios, analysed by contingency X^2 test, showed significant heterogeneity ($X^2 = 36.418$, 11 df, $P < 0.001$). Females however, dominated throughout the year, with peaks in January, March, June and October. The dry season sample of 399 specimens consisted of 121 (30.3%) males and 278 (69.7%) females, giving a 1.0:2.3 sex ratio which was significantly female-biased ($X^2 = 61.777$, 1 df, $P < 0.001$). Similarly, the wet season sample of 705
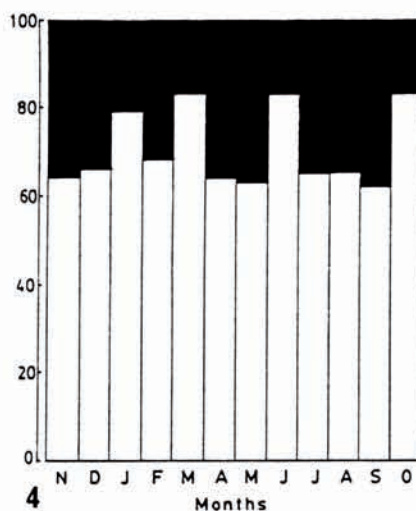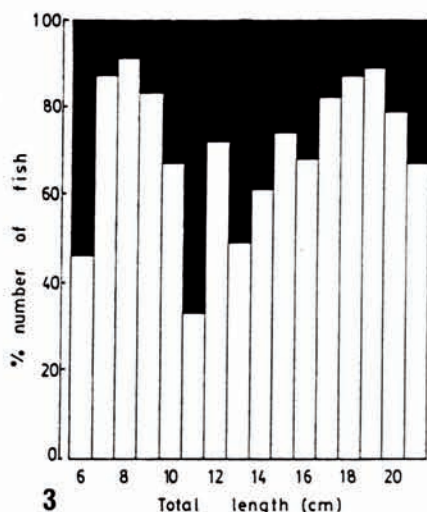
Fig. 3. - Variation in sex ratio with size of *I. africana* in Qua Iboe estuary. Open bars = females; shaded bars = males.
Fig. 4. - Monthly variation in sex-ratio of *I. africana* in Qua Iboe estuary. Open bars = females; shaded bars = males.

specimens comprised 206 (26.2%) males and 499 (70.8%) females, giving a sex ratio of 1.0:2.4 (X^2 = 121.772, 1 df, P < 0.001) in favour of females. Contingency X^2 test indicated homogeneity between the seasonal sex ratio (X^2 = 0.149, 1 df, P > 0.05), but with female predominating during each season.

Gonad morphology
The ovaries are paired organs lying ventrally in the body cavity. The lobes are of unequal sizes, the left lobe being smaller in all specimens; both lobes however, contain oocytes at the same stages of development. In two specimens, the left lobes of the ovaries were totally atrophysed but the remaining right lobes were abnormally large, compensating for the atrophysed lobes. Each ovary opens posteriorly into an oviduct; the two oviducts fuse terminally before opening into the vent.

The testes consist of a pair of small, thin and elongated structures resting on the ventral wall of the body cavity. The left lobes of the testes are smaller than the right lobes. The left and right lobes join posteriorly and then open to the exterior through the vent.

Gonadal morphogenesis
The ovarian maturation scheme comprised four main stages (cf. Lagler, 1978).
Stage I: Immature. The ovaries were very small, opaque and cream in colour; they weighed 0.10-1.10 g; oocytes were visible microscopically but not to the naked eyes.
Stage II: Mature or ripening. Ovaries were enlarged in size and yellowish in colour; they weighed 0.20-2.50 g; minute oocytes were clearly discernible to the naked eyes through the thin and transparent ovary wall.
Stage III: Ripe. Ovaries were fully enlarged, distended and reddish or orange in colour; they weighed 0.40-2.90 g; distinct shiny oocytes were present.

State IV: Spent. Ovaries were brownish in colour, reduced in size and flabby, the oocytes having been discharged; they weighed 0.20-2.50g. Some spent ovaries contained atretic oocytes at various stages of resorption.

Female with resting gonads (ovaries thread-like; oocytes invisible microscopically or macroscopically) were not encountered throughout the study period. Stages in testicular morphogenesis are not here given due to difficulties in delimiting the early and advanced maturation stages.

Maturity size

The smallest female *Ilisha africana* with incipient ovarian development was 6 cm TL., thus delineating the minimum size at sexual maturity. The smallest and largest ripe females encountered measured 6.5 and 21.0 cm TL respectively, with a mean of 15.2 cm TL. The size-frequency distribution of ripe females (Fig. 5) depicts that the majority of sexually active individuals measured 15-17 cm TL. The median size of sexually active females (i.e. length at which 50% of the catch was ripe) for 142 specimens caught during the study period was 15.4 cm TL which agrees closely with the average size of ripe females.

Reproductive investment

Table II shows changes in the average ovary weight and gonadosomatic index during ovarian maturation. Ovary weight was least in immature fish and increased with maturation, peaking in ripe fish and declining in the spent stage. The monthly numbers and sizes of *Ilisha africana* examined for ovarian condition are presented 'n table III. Monthly trends in mean ovary weight (Fig. 6a) ranged between 0.67 and 1.09 g; values < 1.00 g were recorded in December-January and June while values > 1.00 g occurred in all other months. Ovary weight for the dry season (mean ± SD) (mean 0.9i ± 0.17 g; range 0.69-1.06 g) was slightly higher than that of the wet season (mean 0.83 ± 0.14 g; range 0.67-1.09 g).

Table II. - Variations in ovary weight and gonadosomatic index with ovarian maturation in *I. africana*.

Ovarian stage	n	Ovary weight (g)		Gonadosomatic index	
		Mean ± SD	Range	Mean ± SD	Range
Immature	416	0.48 ± 0.18	0.10 - 1.10	2.31 ± 1.20	0.80 - 6.00
Mature	112	1.10 ± 0.35	0.20 - 2.50	4.43 ± 1.74	1.20 - 8.90
Ripe	142	1.51 ± 0.53	0.40 - 2.90	4.89 ± 1.86	2.20 - 10.20
Spent	107	1.14 ± 0.48	0.20 - 2.50	2.18 ± 1.04	1.00 - 5.50

Mean gonadosomatic index increased with ovarian maturation, peaking 'n ripe fish and declining thereafter. The relationship between gonadosomatic index and fish size (11.8-20.5 cm TL) in each ovarian stage is shown in table IV; in each case, there was an inverse relationship between the two variables, thus indicating a decrease in reproductive effort with growth in length. The coefficient of determination for each of these relationships was highest (75.9% in immature fish but declined to a minimum of 20.4% in spent fish).

In gravid females (n = 31), fish total/standard lengths and egg weight were inversely related (Table V; eqns. 6 and 7 respectively), with changes in total/standard lengths accounting for 32.8% and 28.8% of the variations in egg weight respectively. Egg weight was also inversely correlated with fish total and somatic weights (Table V; eqn. 8 and 9 respectively); about 43.9% and 23.7% of
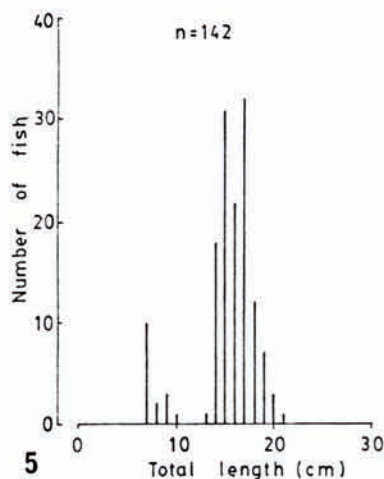
Fig. 5. - Length frequency distribution of breeding *I. africana* in Qua Iboe estuary.
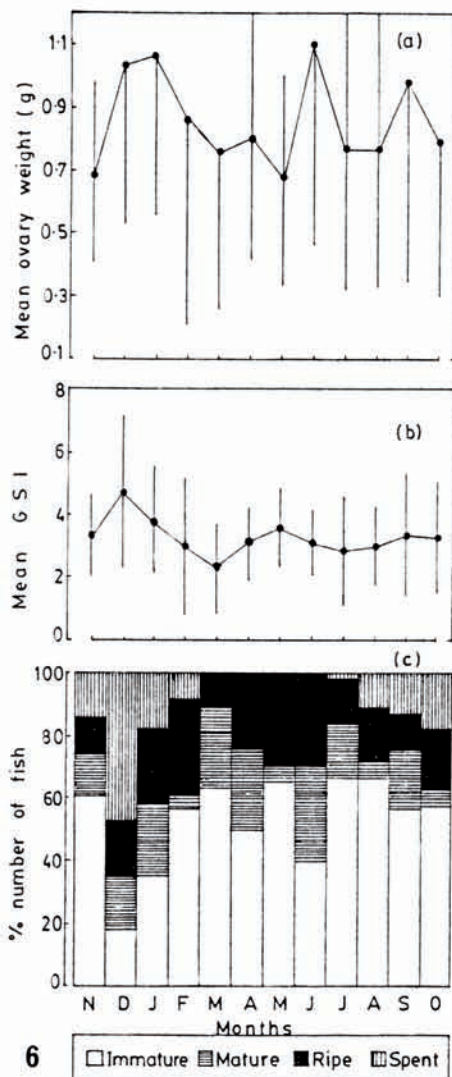

Fig. 6. - Monthly variation in mean ovary weight (a), mean gonadosomatic index (b) and percentage of female *I. africana* (c) at each of the four ovarian maturity stages. Vertical lines represent standard deviations.

the variations in egg weight were explained by changes in fish total and somatic weights respectively. The negative correlation coefficients in the foregoing relationships indicate that the fish invested much less in egg weight with increasing size and weight.

Ovary and egg weights were positively correlated (Table V; eqn. 10); the value of the regression coefficient (b = 0.6168) from the functional equation relating both variables suggests that investment in ovary weight did not result in a proportional increase in egg weight, part of the reproductive investment was probably in ovarian tissue. Egg weight also increased with gonadosomatic index according to equation 11 (Table V) which accounted for 85.6% of the variance in egg weight. The value of the regression exponent (b = 0.8122) indicates that increase in gonadosomatic index produced approximately a proportional increase

Months	n	Total length (cm)
November	52	12.3 - 19.2
December	72	13.2 - 17.0
January	82	12.0 - 19.8
February	70	13.5 - 19.0
March	79	13.0 - 20.0
April	38	12.8 - 19.2
May	35	11.2 - 17.2
June	29	12.6 - 18.7
July	69	12.2 - 18.0
August	84	12.3 - 18.1
September	82	12.3 - 21.0
October	85	12.3 - 20.3

Table III. - Monthly numbers and sizes of *I. africana* examined for ovarian condition.

Table IV. - Functional equations for the relationship between gonadosomatic index (GSI) and fish total length (TL) during ovarian maturation in *I. africana*. + = correlation coefficients (all were significant at P < 0.001); + + = percentage proportion of variation accounted for by the data set.

Ovarian stage	n	Functional equation GSI = a + b (TL)	$(r)^+$	$(\% r^2)^{++}$	Eqn. No
Immature	62	GSI = 8.9013 - 0.4279 (TL)	- 0.871	75.9	(2)
Mature	62	GSI = 16.1222 - 0.7313 (TL)	- 0.830	68.5	(3)
Ripe	62	GSI = 12.9810 - 0.4964 (TL)	- 0.504	25.4	(4)
Spent	62	GSI = 15.0955 - 0.6509 (TL)	- 0.452	20.4	(5)

Table V. - Functional equations for the relationships between egg weight (W_e) and total length (TL), standard length (SL), total weight (W_t), somatic weight (W_s), ovary weight (W_o) and gonadosomatic index (GSI) of *I. africana*. + = correlation coefficient; °P < 0.002; °°P < 0.001.

Relationships	Functional equation ($W_e = aX^b$)	$(r)^+$	Eqn. No
Egg weight vs:			
Total length	$W_e = 7.9403 (TL)^{-1.3114}$	- 0.573°	(6)
Standard length	$W_e = 3.4035 (SL)^{-1.0763}$	- 0.537°	(7)
Total weight	$W_e = 1.9199 (Wt)^{-0.6554}$	- 0.663°	(8)
Somatic weight	$W_e = 1.7805 (Ws)^{-0.6440}$	- 0.685°°	(9)
Ovary weight	$W_e = 0.1845 (Wo)^{-0.6168}$	- 0.487°°	(10)
Gonadosomatic index	$W_e = 0.0612 (GSI)^{-0.8122}$	- 0.925°°	(11)

in egg weight. Both or either of these variables can therefore be reliably used as index(es) of reproductive effort.

Monthly variation in mean gonadosomatic index (Fig. 6b) shows a major peak during the dry season, in December and minor ones during the rains, in May and September. Minimum value occurred in March, during the dry-wet season transition. Reproductive effort during the dry season (mean GSI 3.7 ± 0.7; range 3.0-4.7) was slightly higher than the season value (mean GSI 3.1 ± 0.4; range 2.9-3.6).

Breeding seasonality

Of the 777 adult females examined, 416 (53.5%) were immature, 112 (14.4%) mature, 142 (18.3%) ripe and 107 (13.8%) spent. Monthly trends in occurrence of the ovarian maturation stages and mean gonadosomatic (Fig. 6b, c) were used to established the reproductive seasonality of *Ilisha africana*. No mature fish was caught in May but were present in catches in all other months in proportions ranging from 3.5% in August to 26.3% in April. Ripe females were present on a year-round basis, with minimum proportion (10.8%) in September and maximum (30.0%) in February, May and June. Spent fishes were not encountered in March-June; they were most abundant in December when they constituted 47.2% of the population. The occurrence of mature and ripe females in all months demonstrates an all year-round breeding. The dry season proportion of ripe females (21.6%) was appreciably higher than the wet season value (16.4%).

Monthly variation in mean gonadosomatic index (Fig. 6b) depicts three breeding peaks, the main one in December and subsidiary ones in May and September. Breeding activity was low in November, January-April, June-August and October; minimum intensity occurred in March. Seasonality in gonadosomatic index (see reproductive investment) portrays a higher breeding activity in the dry season than during the rains.

Fat condition

The relationship between fat condition and ovarian maturation of *Ilisha africana* (Table VI) shows highest incidence of fat in immature fish and least at the ripe stage. The proportion of fish with heavy fat reserves (i.e. 20-points on the index scale) peaked in mature fish and was minimum at the spent stage. Fat index ranged from ca. 7.0 in spent fish to 8.4 in immature ones. These results indicate that fat accumulation was highest just before the ovaries ripened and declined thereafter.

Monthly trends in the occurrence of visceral fat deposits (Fig. 7a) varied from 71.3% in August to 100% in April-May. The proportion of fish with heavy fat deposit ranged from 1.4% in February to 21.8% in March; it was < 10% in March-October (wet season) and $\geq$ 10% in November-February (dry season). Average fat index varied between 5.8 in February and 10.3 in March (Fig. 7b).

Table VI. - Variations in incidence of fat deposits and average fat index, with ovarian matu-ration in *I. africana*.

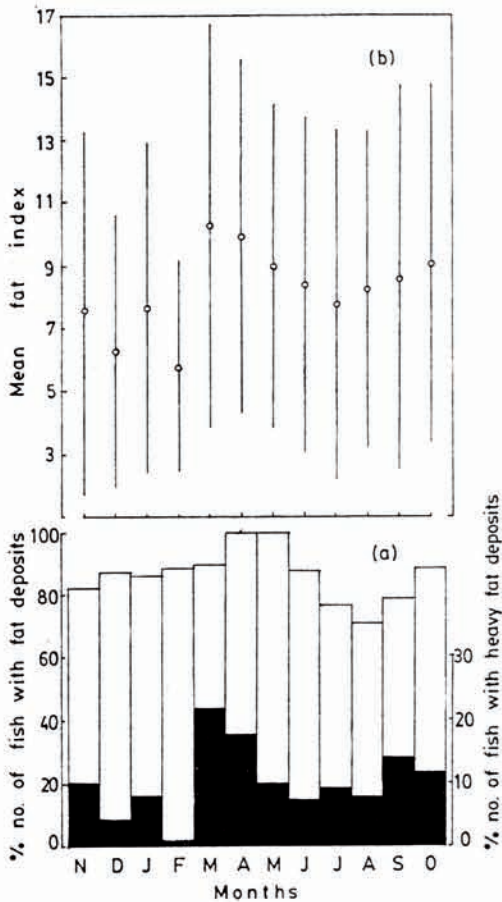| Ovarian stage	n	% incidence of fat deposits	% incidence of heavy fat deposits	Fat index (mean ± SD)
Immature	416	91.2	11.9	8.84 ± 5.59
Mature	112	85.9	15.2	8.89 ± 6.20
Ripe	142	83.9	7.3	7.14 ± 5.32
Spent	107	86.1	4.9	6.98 ± 4.85

Fig. 7. - Monthly variation in incidence of fat deposits (open bars), incidence of heavy fat deposits (shaded bars) (a) and mean fat index (b) of female *I. africana* in Qua Iboe estuary. Vertical lines represent standard deviations.

A comparison of the regimes in gonodosomatic and fat indices (Fig. 6b cf. Fig. 7b) revealed high fat index during the two months preceeding the December and May breeding peaks respectively but was low during these reproductive peaks. The inverse relationship between gonadosomatic and fat indices was statistically significant (r = 0.592, 10 df, P < 0.05) according to the formula:

$$\frac{1}{GSI} = 0.3511 - 0.9885(FI)^{-1} \qquad (12)$$

where $1/GSI$ = coefficient of rate of energy uptake from fat reserves for ovarian development and $(FI)^{-1}$ = coefficient of rate of energy allocation by fat reserves for ovarian development.

Fat index was higher during the rains (mean 8.9 ± 0.9; range 7.8-10.3) than in the dry season (mean 6.7 ± 0.9; range 5.8-7.7). This seasonality regime also shows that the higher dry seasonal breeding activity was preceeded by a heavy fat deposition during the wet season.

Fecundity

The average fecundity of *Ilisha africana* was 6,716 ± 2,975 eggs (range 2,142-12,602 eggs). The relationships between fecundity and total length, standard length, total weight, ovary weight, oocyte weight, gonadosomatic index and condition index were evaluated.

Relationship to length. Mean fecundity relative to total length was 409 ± 127 eggs cm^{-1} TL (range 206-728 eggs cm^{-1} TL) for fish of 7.4-20.3 cm TL (mean 15.8 ± 3.2 cm TL). There was a significant increase in fecundity with total length (r = 0.847, P < 0.002) (Table VII; eqn. 13). Differences in total length accounted for 71.7% of the variation in fecundity. Mean fecundity relative to standard length was 492 ± 145 eggs cm^{-1} SL (range 264-704 eggs cm^{-1} SL) for fish of 5.0-17.3 cm SL (mean 13.2 ± 2.9 cm SL). A significant positive relationship existed between fecundity and standard length (r = 0.843, P < 0.001) (Table VII; eqn. 14), with 71.1% of the variation in fecundity being explained by changes in standard length.

Relationship to body weight. Average fecundity per gram total weight was 226 ± 59 eggs (range 152-405 eggs) for fish weighing 9.3-60.0 g (mean 31.2 ± 14.5 g). Fecundity increased with total weight (r = 0.903, p < 0.001) (Table VII; eqn. 15); about 81.5% of the variation in fecundity was explained by changes in total weight. Mean fecundity per gram somatic weight was 241 ± 71 eggs (range 157-452 eggs) for fish with somatic weight of 10.1-57.7 g (mean 29.8 ± 14.4 g). Fecundity increased with somatic weight (r = 894, P < 0.001) according to eqn. 16 (Table VII) which accounted for 79.9% of the variation in fecundity.

Relationship to ovary weight. Average fecundity per gram ovary weight was 4,861 ± 2,486 eggs (range 1,246-11, 609 eggs) for ovaries weighing 0.5-2.6 g (mean 1.4 ± 0.6 g). There was no significant correlation between fecundity and ovary weight (r = 0.328, P > 0.05), thus portraying a random relationship between both variables. Variations in ovary weight accounted for only 10.8% of the variance in fecundity.

Relationship to oocyte weight. The mean weight of each ripe egg was 0.250 ± 0.133 mg (range 0.080-0.607 mg). Weight of eggs and fecundity were inversely correlated (r = 0.666, P < 0.002) (Table VII; eqn. 17), with changes in the former accounting for 44.4% of the variation in fecundity.

Relationship to gonadosomatic index. Mean gonadosomatic index was 5.7 ± 3.5 (range 2.6-10.2). An inverse relationship existed between fecundity and

Table VII. - Functional equations for the relationships between absolute fecundity (F) and total length (TL), standard length (SL), total weight (W_t), somatic weight (W_s), individual egg weight (W_e), gonadosomatic index (GSI) and condition index (K) of *I. africana*.

Relationships	Functional equation (F = aX^b)	Eqn. No
Fecundity vs:		
Total length	$F = 44.4162 \, (TL)^{-1.7931}$	(13)
Standard length	$F = 112.1368 \, (SL)^{-1.5627}$	(14)
Total weight	$F = 391.2026 \, (W_t)^{-0.8253}$	(15)
Somatic weignt	$F = 481.5489 \, (W_s)^{-0.7767}$	(16)
Egg weight	$F = 2366.4948 \, (W_e)^{-0.6154}$	(17)
Gonadosomatic index	$F = 12514.4510 \, (GSI)^{-0.4658}$	(18)
Condition index	$F = 4799.6244 \, (K)^{-0.7663}$	(19)

gonadosomatic index ($r = -0.574$, $P < 0.002$) (Table VII; eqn. 18); changes in gonadosomatic index accounted for 32.9% of the variation in fecundity.

Relationship to condition index. The condition index of the fish ranged between 0.56 and 1.11, with a mean of 0.78 ± 0.30. Fecundity and condition index were inversely correlated ($r = -0.403$, $P < 0.05$), thus indicating that fish in poor body condition were more fecund than those in better body condition. The exponential function for this relationship (Table VII, eqn. 19) accounted for 16.2% of the variation in fecundity.

DISCUSSION

Observations during the present study revealed that *Ilisha africana* is a monomorphic clupeid owing to the absence of marked sexual dimorphism in size, colour and other morphological features. Females were however, heavier than similarly-sized males due to the heavier ovaries *vis-à-vis* the testes.

The overall sex ratio was significantly female-biased in discord with the finding of Marcus and Kusemiju (1984) that the sex ratio of the population off Lagos coast (Nigeria) did not depart from unity. Given that 1:1 sex ratio indicates the absence of a sex-based dichotomy in longevity (Nikolsky, 1969), the 1.0:2.4 male:female ratio of *Ilisha africana* in the Qua Iboe estuary probably depicts that females live longer than males. Obviously, detailed studies of the age and growth patterns of the sexes are required to reliably ascertain this assertion before it can be accepted with confidence.

From the viewpoint that in a bisexual animal with a 1:1 sex ratio, each female is expected to produce enough egg during her life-span to culminate in a mean of two additional adults (Royce, 1972), it can be inferred that in terms of investment, the strongly female-biased sex ratio of *Ilisha africana* connotes a strategy evolved to ensure increased production of progeny. Additionally, this female preponderance demonstrates that sufficient females are always available to maintain a good population equilibrium (i.e. ability to maintain its numbers) in spite of the prevalence of stochastic environmental constraints such as oil pollution which is a major anthropogenic perturbation of fishes in the Qua Iboe estuary (Umoetok, 1989; pers. obs.).

The ontogenic and temporal regimes in the sex ratio of *Ilisha africana* (Fig. 3 and 4 respectively) probably reflect the natural dynamism in population structure (see Etim *et al.*, 1989). It is however noteworthy that these variations did not substantially influence the general trend of female dominance, thus corroborating the notion of an 'equilibrium population'. Assuming that females continually replace themselves, the constancy in female dominance fits the basic framework of life-history strategy which stipulates that each female must produce in her lifetime, on average, one female that herself survives to reproduce, in order to maintain an equilibrium population (Roff, 1986).

From the overall sex ratio of *Ilisha africana*, it can be reasonably conjectured that during spawning, several females congregate in shoals before broadcasting their eggs into the open water where they are fertilized by milt simultaneously released by few males. Such spawning behaviour is commonplace among other pelagic marine fishes with little or no sexual dimorphism (Royce, 1972).

The stages of ovarian morphogenesis in *Ilisha africana* under study are similar to those described by Marcus and Kusemiju (1984); four major macroscopic stages were identified and, at each stage, the reproductive effort decreased with increasing body size (Table IV), thus designating that small fish invest relatively more energy in ovarian development than larger ones. This suggests the existence of a trade-off between growth and reproductive investment. This emphasis on the allocation of energy resources into reproduction by small fish

vis-à-vis growth may account for the early attainment of sexual maturity (see below) and probably their chances of reproducing before dying especially in the present population which is vulnerable to high mortality resulting from fishing and human-induced environmental perturbations (King, unpubl. data). This type of trade-off between reproductive investment and growth has also been recorded in the tilapiine cichlid, *Tilapia guineensis* (Isaac-Harry, 1986). This strategy is probably evolved when selection pressures operate through high mortality of the prereproductives (juveniles) and high survival of the reproductives and postreproductives.

In *Ilisha africana* which has ovaries containing very little connective tissues (pers. obs.), the individual egg weight can be considered as a realistic measure of reproductive investment. This assertion is supported by the proportional egg weight: gonadosomatic index relationship which accounted for 85.6% of the variance in the functional equation relating both variables (Table V; eqn. 7). Thus by implication, the inverse relationships between egg weight and total/standard lengths and total somatic weights of *I. africana* (Table V) can all be interpreted as supporting evidences for the trade-off between reproductive investment and growth.

Taking the median maturity size as a rough estimate of the optimum maturity size, the latter for female *Ilisha africana* under study was 15.4 cm TL as compared to 13.1 cm TL in the population off Lagos coast (Marcus and Kusemiju, 1984). Since in many fish species the fast growing individuals attain sexual maturity earlier than slow-growers (see Mann, 1980; Mills and Eloranta, 1985a), it is therefore possible that individuals in the population of *I. africana* studied by Marcus and Kusemiju (1984) grow more rapidly and hence mature earlier than those in the Qua Iboe estuary which consequently mature at a slightly larger optimum size. However, considering that this species can grow up to 25.1 cm TL in the present study area (King, unpubl. data), it is clear that it still attains sexual maturity quite early in life.

The current investigation established that *Ilisha africana* bred throughout the year with peaks in December, May and September. Marcus and Kusemiju (1984) similarly found that this species bred all year-round with peaks in May, July, September and December. Protracted breeding in *I. africana* probably ensures that progenies are produced throughout the year, replacing individuals removed by the heavy fishing pressure and other causes of mortality. This is consistent with the concept that environmental constraints which generate a high probability that a given year's progeny will not survive to maturity, favour iteroparity or multiple breeding (McNaughton and Wolf, 1979).

Seasonal plasticity in the breeding of *Ilisha africana* in Qua Iboe estuary depicted higher intensity in the dry season than during the rains. The increased dry season breeding is coincident with the period of heightened abundance of shrimps (Marioghae, 1985), a principal dietary of the fish in the estuary (King *et al.*, in press); thus the newly hatched juveniles find readily available food for growth. The dry season is also the calmest period of the year in the estuary when natural water turbulence, which can adversely affect egg larval survival, has greatly subsided. As noted by Marcus (1982b, c), other allied clupeids (e.g. *Sardinella maderensis* and *Ethmalosa fimbriata*) in the Nigerian coastal waters also exhibit extended breeding, peaking in the dry season. The fact that no female *I. africana* with resting ovaries was encountered during the present investigation indicates that this stage is probably spent by the fish further offshore rather than in the estuary.

In fishes, the development of fat reserves provides readily utilizable energy source for rapid gonad maturation prior to breeding (Bruton, 1979; Welcomme, 1979; Hoogerhoud *et al.*, 1983). Thus peak lipid accumulation in *Ilisha africana* occurred just before the ovaries ripened and 1-2 months preceeding the breeding peaks and were utilized during spawning, a regime analogous to that of the haplochromine cichlid, *Haplochromis iris* in Lake Victoria, Tanzania (Hoogerhoud *et al.*, 1983). Soon after each breeding peak, there was a sharp increase in fat in-

dex as lipid reserves were replenished ready for the onset of the next breeding peak.

The results of the gonadosomatic index: fat index relationship for *Ilisha africana* (summarized in eqn. 12: r = - 0.592) demonstrate that associated with increase in reproductive investment, is a corresponding decline in the proportion of visceral fat reserve, a pattern showing a physiological trade-off in lipid energy reserve and presumably other energy reserves (e.g. in liver and muscles) that are related to increasing reproductive investment. Comparative evidences for this type of trading-off lipid energy reserve for increased reproductive investment are provided by Hoogerhoud *et al.*, (1983) for the fish, *Haplochromis iris* and Brough and Dixon (1989) for the aphid insect, *Megoura viciae*. Equation 12 is inappropriate for general use for predictive purposes since energy source (fat reserve) was determined semi-quantitatively on an arbitrary scale. Nevertheless, it is important as an empirical surrogate measure because of the explicit trend it generates in relative energy allocation to reproductive investment.

The present fecundity estimate of *Ilisha africana* (mean 6,716 eggs; range 2,142-12,602) in slightly high compared to 2,089-11,687 eggs (mean 5,227) produced by the same species (size 14.0-25.4 cm TL) off Lagos coast (Marcus and Kusemiju, 1984). This difference, which can be used for stock discrimination (cf. Alvarez-Lajonchere, 1982), is attribuable to a number of factors including the available food resource quality/quantity, sizes of specimens examined, seasons and specific environmental conditions. Disparities in fecundity among populations of a given fish species may be considered as adaptations to different environmental conditions that produce higher or lower survival opportunities for the species (see Weisel *et al.*, 1973). This contention probably explains the higher fecundity of *I. africana* in the Qua Iboe estuary which is subject to relatively high man-induced environmental stress.

The fecundity: total length relationship for *Ilisha africana* of Qua Iboe estuary gave a regression coefficient (b = 1.7931) denoting that fecundity increased at a rate about the square of the length, probably as a consequence of the importance of fish surface area as a determinant of fecundity fluctuations in this population; conversely, Marcus and Kusemiju (1984) obtained b = 3.291, indicating that fecundity depends strongly on body volume in the population off Lagos coast. The fecundity of *I. africana* from Qua Iboe estuary increased with total and somatic weights as expected (Bagenal and Braum, 1978). The regression coefficient for the fecundity: total weight relationship (b = 0.825) is comparable to that obtained by Marcus and Kusemiju (1984) (b = 1.049). It thus seems that total weight is a more stable morphometric attribute explaining the variations in fecundity *vis-à-vis* body length. The random relationship between fecundity and ovary weight in *I. africana* parallels the record of Campbell (1987) on *Tilapia guineensis*. The precise reason and consequence of this random relationship are uncertain.

Since the fecundity of *Ilisha africana* increased with body weight and egg weight is a function of body weight, the total egg weight is proportional to the female weight and can be assumed to roughly represent the reproductive drain on the fish (cf. Fryer and Iles, 1972). This probably explains the positive oocyte weight versus ovary weight and oocyte weight versus gonadosomatic index relationships in *I. africana* (Table V). The inverse function between oocyte weight and fecundity (Table VII) (cf. inverse egg number: egg size relationship in *Leuciscus leuciscus*: Mann and Mills, 1985) shows that less fecund females tend to produce heavier eggs than more fecund one. The fecundity cost is there assumed to be associated with high egg quality (i.e. weight).

In as much as oocyte weight of *Iliana africana* increased with gonadosomatic index (Table V), the inverse fecundity, gonadosomatic index relationship (Table VII), is as expected and suggests that fish with high reproductive effort did not necessarily invest proportionally in egg production. Emphasis on reproductive effort was therefore on oocyte quality rather than

number. The result suggests the existence of a trade-off between fecundity and egg weight. This is comparable to the trade-off between egg number and size in some haplochromine cichlids from Lake Victoria (Goldschmidt, 1989a, b). The specific adaptive significance of trading-off egg number for quality in *I. africana* is unclear but may presumably ensure egg survival by enabling it to float in mid-water rather than at the surface where it would be exposed to more severe stochastic environmental perturbations such as turbulence induced by boat traffic and oil slick from a variety of source linked with petroleum exploitation; the egg, by virtue of its weight, is also probably prevented from being easily washed ashore. Previous studies (e.g. Mann and Mills, 1985; Mills and Eloranta, 1985b; Goldschmidt and Witts, 1989) have demonstrated that egg quality (size) is closely associated with the size and survival of the fish larvae that hatch.

Using the condition index as a morphometric interpretation of the overall physiological state of a fish, the inverse fecundity, condition index relationship in *Ilisha africana* (Table VII), may be construed as the mathematical expression denoting that increased oocyte production is at the expense of body condition (cf. Roff, 1982). Such a strategy involving a physiological trade-off could select for a much reduced reproductive life-span and overall longevity (here 5 yr: Marcus, 1982a) due to physiological stress imposed by sacrificing body condition (i.e. metabolizing somatic tissue to subsidize the energy requirements of ovarian development and egg production) in order to increase or optimize egg production. Other teleosts known to adopt this strategy of reproductive energy allocation include the stickleback, *Gasterosteus aculeatus* and American plaice, *Hippoglossoides platessoides* (see Roff, 1982, 1986).

A comparison of the coefficients of determination for the relationships between fecundity and total length (71.7%), standard length (71.1%), total weight (81.5%), somatic weight (79.9%), ovary weight (10.8%), oocyte weight (44.4%), gonadosomatic index (32.9%) and condition index (16.2%) buttresses the earlier assertion that total weight is an important morphometric attribute explaining variations in the fecundity of *Ilisha africana*. This was closely followed by somatic weight, total and standard lengths. Each of ovary weight, gonadosomatic and conditions indices contributed < 40% to explaining the observed variance in fecundity.

The reproductive traits of a fish species are often incorporated into the functional measures of the relative fitness patterns (i.e. r- and k-selection pressures) of life-history strategies. The r-selected species are typified by early onset of reproduction (i.e. small size/age at sexual maturity), high reproductive investment/output, semelparity and short life-span while k-selected species are characterized by delayed onset of reproduction (i.e. large size/age at sexual maturity), low reproductive investment/output, iteroparity and high longevity (see McNaughton and Wolf, 1979; Warren and Liss, 1980; Bone and Marshall, 1982). In its small size at first reproduction, year-round breeding, high fecundity and short life-span, *Ilisha africana* of the Qua Iboe estuary can be classed as an r-selected species. Nevertheless, there are indications that unlike typical r-selected species, *I. africana* exhibits iteroparity rather than semelparity. This species is thus like *Gasterosteus aculeatus* which incorporates both the r- and k-selected traits in its life-history (O'Hara and Penczak, 1987). Recognizing that the r- and k-selection pressures can be considered as representing the extremes of a continuum of methods for maximizing reproductive success (MacNaughton and Wolf, 1979), the existence of transitional fishes that include both r- and k-selected attributes in their life-histories (due to overlaps along the continuum) is not surprising.

It is shown in the present study that the reproductive life-history of *Ilisha africana* involves trade-offs between resources embodied in growth and fitness components of reproductive strategy. The results are consistent with Roff's (1983) hypothesis that the reproductive strategies of teleosts are determined in part by trade-off between growth and reproduction. The approach (whereby one fitness

component is varied and the response of the other(s) measured) used in delineating trade-off in the reproductive strategy of *I. africana* (i) egg weight *vs* body size and weight, (ii) gonadosomatic index *vs* body size, (iii) gonadosomatic index *vs* fat index, (iv) fecundity *vs* egg weight, gonadosomatic index and condition index) has yielded information which allow for the making of useful deductions. It is here hypothesized that the reproductive life-history of *I. africana* in the Qua Iboe estuary which involves an integration of the r- and k-selection pressures, can be viewed as the end result of a strategy designed to equilibrate the optimization of reproductive success (fecundity) and enhanced potential of progeny survival (in term of egg quality) for future reproduction. This is inconsistent with the concept of trade-off between fitness components which presumes that increasing one fitness components (e.g. fecundity) often leads to a decrease in another (e.g. survival which is considered as the cost of reproduction (see Møller *et al.*, 1989). This non-conformity should however, be regarded as "tentative" since it can be argued that the present use of egg quality to reflect progeny survival is not entirely convincing. Studies on juvenile survival (from egg to emergent adult) will thus provide an interesting line of further research into reproductive strategy of *I. africana* in the Qua Iboe estuary.

REFERENCES

ALVAREZ-LAJONCHERE L., 1982. - The fecundity of mullet (Pisces, Mugilidae) from Cuban waters. *J. Fish Biol.*, 21: 607-613.

BAGENAL T.B. & E. BRAUM, 1978. - Eggs and early life history. *In:* Methods for assessment of fish production in fresh waters (3rd ed.), pp. 101-136. International Biological Programme Handbook No. 3. Blackwell Scientific Publications Ltd.

BAILEY N.T.J., 1959. - Statistical methods in biology. The English Language Book Society and the English Universities Press Ltd, 200 pp.

BONE Q. & N.B. MARSHALL, 1982. - Biology of fishes. Blackie and Son Ltd, 253 pp.

BROUGH C.N. & A.F.G. DIXON, 1989. - Interclonal trade-off between reproductive investment and size of fat body in the vetch aphid, *Megoura viciae* Buckton. *Funct. Ecol.*, 3: 747-751.

BRUTON M.N., 1979. - The breeding biology and early development of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with a review of breeding in species of the subgenus *Clarias (Clarias)*. *Trans. Zool. Soc. Lond.*, 35: 1-45.

CAMPBELL D., 1987. - A review of the biology and culture of *Tilapia guineensis*. African Regional Aquaculture Centre, Port Harcourt, Nigeria. *ARAC/87/WP/3.*, 15 pp.

ENYENIHI U.K., ADEYEMI-WILSON O.A. & A.I. OBIEKEZIE, 1988. - Ecological parameters of the mangrove swamp forest of the Cross River State - Baseline study. *In:* The petroleum industry and the Nigerian environment, pp. 228-239. The federal ministry of works and housing and the petroleum inspectorate, Nigerian National Petroleum Corporation, Surulere, Lagos, Nigeria.

ETIM L., ETCHERI I. & O. UMOREN, 1989. - Aspects of the reproductive biology of *Tilapia guineensis* (Perciformes: Cichlidae) in Editas pond, Nigeria. *J. Afr. Zool.*, 103: 127-134.

FAGADE S.O. & C.I.O. OLANIYAN, 1973. - The food and feeding interrelationship of the fishes in the Lagos lagoon. *J. Fish Biol.*, 5: 205-225.

FRYER G. & T.O. ILES, 1972. - The cichlid fishes of the great lakes of Africa: their biology and evolution. Oliver and Boyd, Edinburgh, 641 pp.

GOLDSCHMIDT T., 1989a. - Reproductive strategies of haplochromine species (Pisces, Cichlidae) from Lake Victoria. *In:* An ecological and morphological field study on the haplochromine cichlid fishes (Pisces, Cichlidae) of Lake Victoria, pp. 93-119. Thesis, Rijksuniversiteit, Leiden.

GOLDSCHMIDT T., 1989b. - Reproductive strategies, subtrophic niche differentiation and the role of competition for food in haplochromine cichlids (Pisces) from Lake Victoria, Tanzania. *Annls Mus. Roy. Afr. Centr., Sc. Zool.,* 257: 119-132.

GOLDSCHMIDT T. & F. WITTE, 1989. - Reproductive strategies of five zooplanktivorous haplochromine species (Pisces, Cichlidae) from Lake Victoria. *In:* An ecological and morphological field study on the haplochromine cichlid fishes (Pisces, Cichlidae) of Lake Victoria (Goldschmidt T., ed.), ch. 2: 53-90. Thesis, Rijksuniversiteit, Leiden.

HOOGERHOUD R.J.C., WITTE F. & C.D.N. BAREL, 1983. - The ecological differentiation of two closely resembling *Haplochromis* species from Lake Victoria (*H. iris* and *H. hiatus*; Pisces, Cichlidae). *Neth. J. Zool.,* 33(3): 283-305.

ISAAC-HARRY S.L., 1986. - Studies on reproduction of *Tilapia guineensis.* Thesis, African Regional Aquaculture Centre, Port Harcourt, Nigeria.

KING R.P., UDOIDIONG O.M., EGWALI E.C. & N.A. NKANTA. - Some aspects of the trophic biology of *Ilisha africana* (Teleostei: Pristigasterinae) in Qua Iboe estuary, Nigeria. *J. Afr. Zool.,* 105: (in press).

LAGLER K.F., 1978. - Capture, sampling and examination of fishes. *In:* Methods for assessment of fish production in fresh waters (3rd ed.), pp. 7-47. International Biological Programme Handbook No. 3. Blackwell Scientific Publications Ltd.

MANN R.H.K., 1980. - The growth and reproductive strategy of the gudgeon, *Gobio gobio* (L.) in two hard-water rivers in southern England. *J. Fish Biol.,* 17: 163-176.

MANN R.H.K. & C.A. MILLS, 1975. - Variations in the sizes of gonads, eggs and larvae of the dace, *Leuciscus leuciscus. Env. Biol. Fish.,* 13(4): 277-287.

MARCUS O., 1982a. - The biology of the clupeid, *Ilisha africana* (Bloch) of the Nigerian coast. Thesis, University of Lagos, Nigeria.

MARCUS O., 1982b. - The biology and fishery of *Sardinella maderensis* (Lowe, 1839) caught off the Nigerian coastal waters. *In:* Annual report, pp. 9-10. Nigerian Institute for Oceanography and Marine Research, Victoria Island, Lagos.

MARCUS O., 1982c. - The biology of the West African shawa, *Ethmalosa fimbriata* (Bowdich) found in Nigerian coastal waters. *In:* Annual report, pp. 10-11. Nigerian Institute for Oceanography and Marine Research, Victoria Island, Lagos.

MARCUS O., 1986. - Food and feeding habits of *Ilisha aficana* (Bloch) off the Lagos coast, Nigeria. *J. Fish Biol.,* 29: 671-683.

MARCUS O. & K. KUSEMIJU, 1984. - Some aspects of the reproductive biology of clupeid, *Ilisha africana* (Bloch) off the Lagos coast, Nigeria. *J. Fish Biol.,* 25: 679-689.

MARCUS O., ISEBOR C.E. & M.A. OYEBANJI, 1984. - State of the coastal artisanal fisheries in Ondo and Cross River States. *In:* Annual report, pp. 38-39. Nigerian Institute for Oceanography and Marine Research, Victoria Island, Lagos.

MARIOGHAE I.E., 1985. - Review of research on penaeid schrimps in Nigeria. *In:* The mangrove ecosystem of the Niger Delta, pp. 212-225. Publications Committee, University of Port Harcourt, Nigeria.

McNAUGHTON S.J. & L.L. WOLF, 1979. - General ecology. Holt, Rinehart and Winston, 702 pp.

MILLS C. & A. ELORANTA, 1985a. - The biology of *Phoxinus phoxinus* (L.) and other littoral zone fishes in Lake Konnevesi, Central Finland. *Ann. Zool. Fennici,* 22: 1-12.

MILLS C. & A. ELORANTA, 1985b. - Reproductive strategies in the stone loach, *Noemacheilus barbatulus. Oikos,* 44: 341-349.

MØLLER H., SMITH R.H. & R.M. SIBLY, 1989. - Evolutionary demography of a bruchid beetle. II. Physiological manipulations. *Funct. Ecol.* 3: 683-691.

NIKOLSKY G.V., 1963. - The ecology of fishes. Academic Press Inc. (London) Ltd, 352 pp.

NIKOLSKY G.V., 1969. - The theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources. Oliver and Boyd, Edinburgh, 323 pp.

O'HARA K. & T. PENCZAK, 1987. - Production of three-spined stickleback, *Gasterosteus aculeatus* L., in the River Weaver, England. *Freshwat. Biol.,* 18: 353-360.

ROFF D.A., 1982. - Reproductive strategies in flatfish: a first synthesis. *Can. J. Fish. Aquat. Sci.,* 39: 1686-1698.

ROFF D.A., 1983. - An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.,* 40: 1395-1404.

ROFF D.A., 1986. - Predicting body size with life history models. *BioScience,* 36(5): 316-323.

ROYCE W.F., 1972. - Introduction to the fishery sciences. Acad. Press, New York and London, 351 pp.

TAHAL CONSULTANTS (Nigeria) Ltd, 1979. - Qua Iboe River Basin prefeasibility study. Cross River Basin Development Authority, Nigeria, 2, Annex II: A-1-14.

TOBOR J.G., 1966. - Meristic counts of some important marine fishes in Lagos. *Bull. I.F.A.N.*, Series A., 28: 259-275.

UMOETUK E.J., 1989 - The effects of offshore oil exploration on fishing in Ibeno area of Akwa Ibom State (Nigeria). Thesis, University of Cross River State, Uyo, Nigeria.

WARREN C.E. & W.J. LISS, 1980. - Adaptation to aquatic environments. *In:* Fisheries management (Lackey R.T. & L.A. Nielsen, eds.), pp. 15-40. Blackwell Scientific Publications.

WEISEL G.F., HANZEL D.A. & R.L. NEWELL, 1973. - The pygmy whitefish, *Prosopium coulteri,* in western Montana. *Fish. Bull.,* 71(2): 589-596.

WELCOMME R.L., 1979 - Fisheries ecology of foodplain rivers. Longman Group Ltd., London. 317 pp.

WILKINSON D.R. & J.W. JONES, 1977. - The fecundity of dace, *Leuciscus leuciscus* (L.) in Emral Brook, Clwyd, North Wales, *Freshwat. Biol.,* 7: 135-145.

WILLIAMS F., 1968. - The Guinean trawling survey report 1. *Publication 99: OAU/STRC,* Lagos. 282 pp.